Erratum: For Synthiloboramphus read Synthliboramphus

Morphological variation and species limits in Murrelets of the genus *Endomychura*

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ABSTRACT.—Species limits in *Endomychura* have been a matter of dispute. Recent field studies in Baja California have shown that the probable breeding ranges of two of the three currently recognized taxa are more extensive than has been realized, and that all three taxa occur on the San Benito Islands during the nesting season. Morphological data indicate that Craveri's Murrelet *(E. craveri)* is acting as a distinct species with respect to both forms of Xantus' Murrelet *(E. hypoleuca)*. *Endomychura h. hypoleuca* and *E. h. scrippsi* are exceptionally well-marked forms and differ significantly in size and plumage characters. They apparently hybridize on the San Benitos, but the limited data suggest that interbreeding is not random, that gene flow between the two is reduced, and that isolating mechanisms are being tested. Face pattern and bill shape may be the most effective isolating mechanisms as they are sufficient to provide a rapid means of species recognition. Differences in face pattern and bill shape among the several populations may constitute a complex case of character displacement. Further studies in the area of overlap are needed to determine the extent of hybridization and whether a third species of *Endomychura* should be recognized. Color patterns of the downy young support the view that *Endomychura* is most closely allied to *Synthiloboramphus.*

The beginning of ornithological explorations in Baja California in the mid-1850's resulted in the description of many taxa, including two new species of alcids. Xantus' Murrelet *(Endomychura hypoleuca)* was described by Xantus in 1859 from a specimen taken off Cabo San Lucas. Shortly thereafter, in 1865, Salvadori described a similar species, Craveri's Murrelet *(Endomychura craveri)*, from Natividad Island on the west side of the Baja California peninsula. (Although the A. O. U. [1957] has recognized Isla Raza in the Gulf of California as the type locality of *craveri*, DeLong and Crossin [MS] argue convincingly that the Natividad Island designation is correct.)

The taxonomic ranking of *craveri* soon came under fire. Coues (1884) thought it "questionably distinct" from *hypoleuca*. Ogilvie-Grant (1898) suggested that it might be the breeding plumage of *hypoleuca*, Ridgway (*in* Anthony, 1900) speculated that the forms represented different sexes or color phases of the same species. Anthony (1900) effectively refuted these views but speculated, in turn, that *craveri* might be the immature plumage of *hypoleuca*, a position supported by Grinnell (1915) after "a hasty glance at the material in the Museum of Vertebrate Zoology."

Van Rossem (1926) made the first critical study of the problem. He showed that *craveri* was not an age variant of *hypoleuca* but was a "perfectly distinct" form, whose breeding range was confined, so far as known, to the Gulf of California; *hypoleuca* breeds on islands of the Pacific coast. Grinnell (1928) relented, writing; "The systematic status of the Craveri Murrelet has been much discussed . . .; the last and seemingly final word is by van Rossem (1926a, p. 80)."

Grinnell's hopes, however, were in vain, for van Rossem (1939) changed his mind. Early in 1939, Green and Arnold showed that *E. hypoleuca* was divisible into two well-marked subspecies, *E. h. hypoleuca*, from Guadalupe Island, and *E. h. scrippsi*, from the near-shore islands of California and northern Baja California. For his 1926 paper, van Rossem had examined only one specimen from Guadalupe. He now (1939) examined specimens from the San Benito Islands — another area which he had ignored in his earlier paper — and after a cursory study described a new form, *E. h. pontilus*, that seemed intermediate between *craveri* and *hypoleuca (sensu lato)*. This convinced him (1939: 442) that "there is no longer the slightest reason to consider the two supposed species as other than geographic races. Further evidence of intergradation is provided by a specimen . . . from Natividad Island . . . that is exactly intermediate in all particulars."

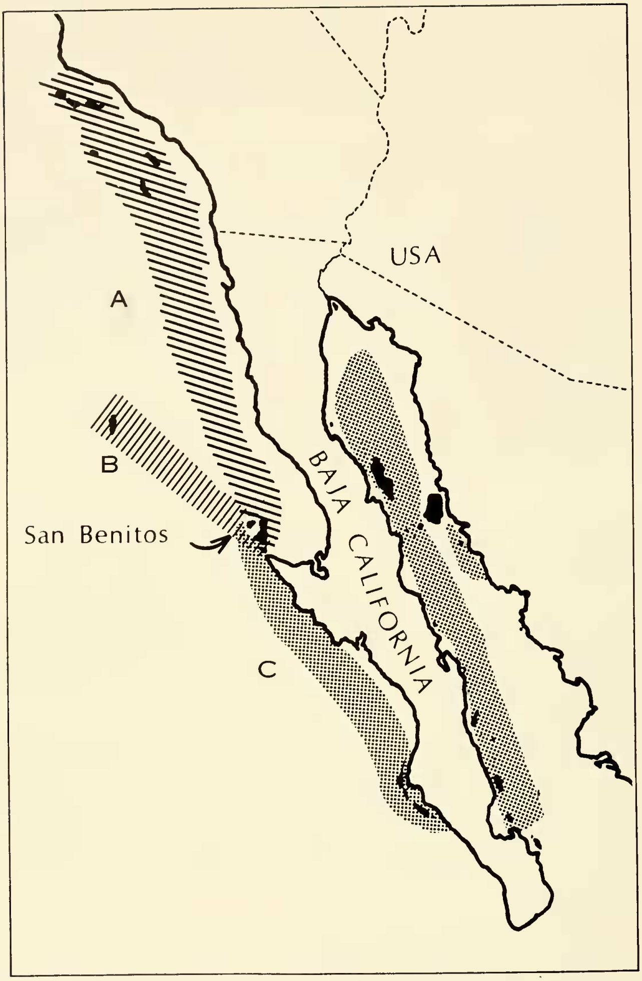

Figure 1. Probable breeding distribution of *Endomychura* murrelets: *E. h. scrippsi* (A); *E. h. hypoleuca* (B); *E. craveri* (C). The three forms are sympatric on the San Benito Islands.

At this point, one might have expected the case to be closed and that taxonomists would have adopted a consistent treatment of variation in *Endomychura*. That was not the case. The A. O. U. Check-List committee (Wetmore, et al., 1944) took no action, then or subsequently, on van Rossem's new race but accepted that proposed by Green and Arnold. This was surprising, for van Rossem was a member of the committee, and it is hard to believe that he would have forgotten to request formal consideration for one of his own creations. Confusion resulted. By ignoring van Rossem (1939), the A. O. U. was forced to continue to recognize two species of *Endomychura*. On the other hand, the compilers of the Mexican Check-List (Friedmann, Griscom, and Moore, 1957) followed van Rossem and recognized one polytypic species. But, inexplicably, they did not recognize, comment on, or even synonymize *E. h. pontilus*, the supposed connecting link!

The early taxonomists were severely limited by a fragmentary knowledge of the breeding range of the several forms and by extremely limited specimen collections of *hypoleuca* from Baja California. That the mid-peninsula islands of the west coast might prove critical in understanding relationships in *Endomychura* was anticipated by Bancroft (*in* Dawson, 1923), who speculated that "intergradation . . . probably occurs . . . in the vicinity of Cedros Island." Recent field work in this area, by ourselves and others, has resulted in the collection of new material from Guadalupe Island and the San Benitos Islands. We now recognize that birds of the *craveri* type occur along the southern half of the west coast of Baja California during the breeding season, and furthermore that all three forms, *craveri, h. hypoleuca,* and *h. scrippsi,* occur synchronously on the San Benito Islands in spring. These discoveries have led us to review morphological variation in the several populations, with special reference to the San Benitos.

DISTRIBUTION DURING THE BREEDING SEASON: EVIDENCE OF SYMPATRY

Endomychura hypoleuca presumably once nested on all of the islands along the coast of Southern California and Baja California, from San Miguel in the north to the San Benitos in the south. We know of breeding records for the following islands[1]: Prince Islet, San Miguel Island (specimens USNM); Anacapa Island (specimens SDSNH; eggs collected, Peyton, 1913; Wright and Snyder, 1913); Santa Barbara Island (specimens LACMNH; eggs collected, Willet, 1912; G. Hunt, pers. comm.); San Clemente Island (Jehl and G. McCaskie, adult and downy chick in waters adjacent to island in 1968); Los Coronados (specimens SDNHM; Lamb, 1909; Howell, 1917; pers. obs.); Todos Santos Islands ("on and about" island, Kaeding, 1905; broken egg, birds eaten by cats, Van Denburgh, 1924); San Martín Island ("on and about" island, Kaeding, 1905); San Benito Islands (specimens Carnegie Mus., SDNHM; Kaeding, 1905; pers. obs.); and islets at Guadalupe Island (specimens SDNHM, USNM; Green and Arnold, 1939: pers. obs.). Populations on some islands, (Todos Santos, San Geronimo, San Martín, the main island of Guadalupe) have apparently been extermined by rats or feral cats (e.g., Howell, 1912; Van Denburgh, 1924). The current status of populations on most islands is not known.

Various authorities (e.g., A. O. U., 1957) list Natividad Island as a breeding station; this presumption is based on Lamb's (1927) *winter* observations of "pairs" of murrelets alleged to be *hypoleuca* at sea near the island. Murrelets (species?) probably have nested there, but there is no evidence of that event. Natividad is currently infested with feral cats and we doubt that nesting murrelets could survive. We know of no sight records or specimens of *hypoleuca* during the breeding season south of Turtle Bay. Studies between Natividad and Magdalena Bay and especially on Islas San Roque and Asuncion are needed.

Endomychura craveri has been generally thought to breed only in the Gulf of California (see DeWeese and Anderson MS for a review of nesting areas) but evidence is accumulating that its range is not so restricted. Anthony (1900) reported "a number of family parties" of murrelets off Magdalena Bay in June 1897; although he presumed these were *hypoleuca,* his only specimen was of a flightless adult *craveri*! (It was this specimen [now Carnegie Mus. no. 22973], which he identified as a juvenile *hypoleuca,* that led to his speculation that *craveri* was the juvenile of *hypoleuca).* More recent observations also suggest breeding in the Magdalena Bay area. On a transect between Cabo San Lucas and San Diego in mid-June 1974, we saw 12 murrelets, including several pairs, between Cabo San Lucas and the San Benitos; the eight that could be identified were *craveri.* On a southward transect through the same area, in early April 1975 Jehl and K. E. Stager saw five murrelets off Turtle Bay on 5 April and the several that could be identified were *craveri.* On 6 April they saw 7 pairs of murrelets, all *craveri,* 5 to 8 miles off Santa Margarita Island, Magdalena Bay.

[1]Listed here are selected primary references that substantiate breeding at a particular locality.

There are also records of *craveri* off northern Baja California during the breeding season. Jehl saw a single bird 4 mi S of Los Coronados on 20 February 1972, and another 4 mi S of Point Loma, San Diego, on 6 June 1969. On a transect between San Diego and the San Benito Islands in early April 1974, Jehl saw a pair of *craveri* (but no other murrelets) 21 mi S of San Martín Island on 4 April. On 8 April he saw 30 murrelets in the northeast corner of Vizcaino Bay; these included 6 pairs and 1 single *craveri*, 1 pair of *hypoleuca*, and 15 unidentified. Specimens from this area, all of which were taken aboard ship, are: NW end Cedros Island, 27 February 1941 (LACMNH 50594); Cabo Colnett, 2 March 1949 (LACMNH 51845); and San Martín Island, 13 April 1951, largest ovum 4 mm (LACMNH 51879).

The most convincing evidence that *craveri* breeds along the west coast of Baja California comes from the San Benito Islands. In late April 1968, members of the Smithsonian Institution's Pacific Ocean Biological Survey Program collected 19 murrelets, all with enlarged gonads, from many that flew aboard their ship at night: seven were *craveri* and 12 *hypoleuca*, including *E. h. hypoleuca* and *E. h. scrippsi*. In late May 1971 Jehl examined 27 murrelets that flew aboard at West Benito Island; five were *craveri*, and both races of *hypoleuca* were present among the remainder. A total of ten individuals of the three forms were collected; their gonads were enlarged.

In summary, observations of Craveri's Murrelets, some obviously paired, along the west coast of Baja California during the breeding season provide presumptive evidence of nesting north to the San Benitos-Cedros area and perhaps beyond. The population at the San Benitos may comprise 20–30% *craveri*, and also includes both forms of *hypoleuca*. Limited field observations suggest that where *craveri* comes into contact with *hypoleuca* pairing is assortative. Finally, Anthony's 1897 observations indicate that the presence of *craveri* on the west coast of Baja California is not the result of a recent range expansion.

The probable breeding ranges of the several forms are shown in Figure 1.

GEOGRAPHIC VARIATION

We examined approximately 370 specimens of *Endomychura* from the following institutions: San Diego Natural History Museum; California Academy of Sciences; University of California, Los Angeles; American Museum of Natural History; Museum of Vertebrate Zoology, University of California; Los Angeles County Museum of Natural History; United States National Museum; Burke Memorial Museum, University of Washington. These collections include much new material from the San Benito Islands and Guadalupe Island that has not been analyzed previously.

Specimens were sorted according to the criteria of van Rossem (1926) and Green and Arnold (1939). Briefly, *E. craveri* may be characterized as a small black-and-white murrelet with a long, slender bill; the underwing is usually grayish, but varies from whitish (though never pure white) to dark sooty gray: the inner vane of the outer primaries is brownish. Birds in fresh plumage have a brownish cast to the black back feathers, which is often evident even in worn nesting birds. The dark feathers extend onto the sides of the neck forming a partial collar. Flank feathers are uniformly dark.

E. hypoleuca is slightly larger, with a shorter, stouter bill; the underwing is whitish, sometimes flecked with a few dark feathers; the inner vane of the outer primaries is whitish. Freshly-plumaged birds have a blue or blue-gray tinge to the back, and the flank feathers may be tipped with white. The face pattern varies geographically (see below).

For each species samples were separated into probable breeding and nonbreeding subsamples. We have no data on how far murrelets may range from their nesting area and assume that specimens taken in the vicinity of a known breeding island in the breeding period (roughly February through June) are representative of the local population.

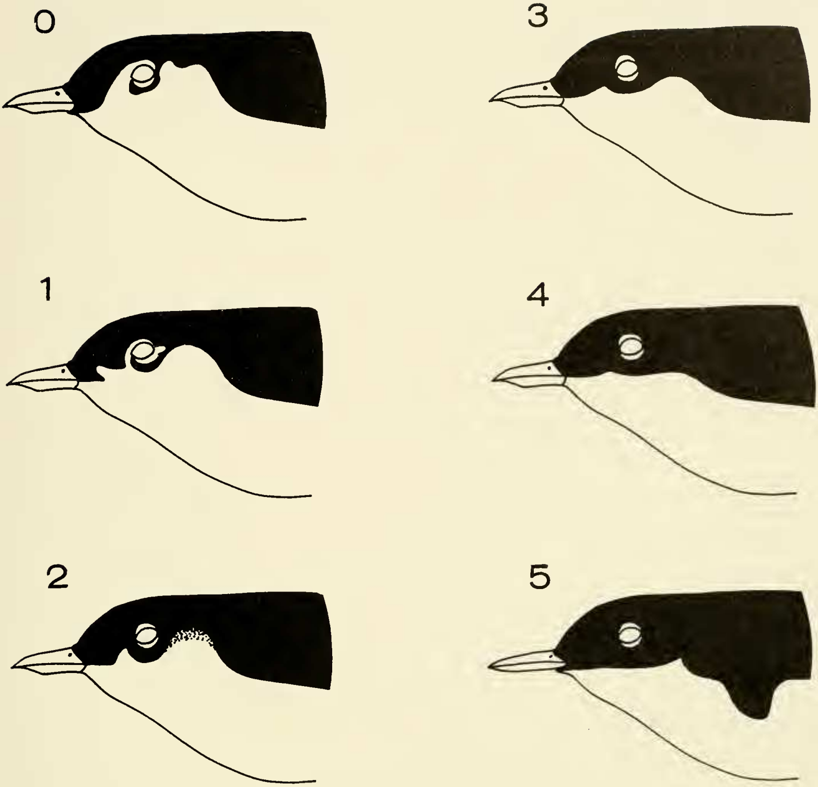

Figure 2. Face and throat pattern variation in *Endomychura hypoleuca* (0-4) and *E. craveri* (5), drawn from specimens collected on the San Benito Islands, 26 May 1971.

We emphasize that localities given on specimen labels are too often imprecise. Murrelets are notorious for landing on ships, but labels rarely indicate whether a specimen collected, say, at "Guadalupe Island" was taken at sea near the island, from a nesting burrow, or flew aboard at night. Future workers are cautioned to record these data precisely.

The following measurements were taken: exposed culmen; bill depth at gonys, chord of wing, and length of tarsus. Variation in face pattern was coded as shown in Figure 2. The ratio of bill depth to bill length was calculated. Mensural characters were not recorded from all specimens, due to time limitations, but all specimens were carefully checked for evidence of intergradation.

Endomychura hypoleuca

Measurements of Xantus' Murrelet are given in Table 1. Size varies clinally in this species, birds from northern colonies having shorter and deeper bills but longer wings and tarsi than those from farther south. Weight data, though few, also suggest that northern birds are bigger. In northern populations (Channel Islands, Los Coronados) the face pattern is exclusively dark (Classes "3" and "4", Figure 2), whereas whiter patterns (Classes "0" and "1") characterize the

TABLE 1. Measurements of Xantus' Murrelet *(Endomychura hypoleuca)*

Area	Male				Female			
	No.	Range, mean and S.E.	S.D.	C.V.	No.	Range, mean and S.E.	S.D.	C.V.
Exposed Culmen								
1. Northern Channel Islands	10	15.6–19.3(17.05) ± 0.33	1.05	6.15	7	16.8–19.0(18.04) ± .44	1.17	6.48
2. Southern Channel Islands	1	16.5			2	18.3–18.7(18.5)		
3. Los Coronados	41	16.3–19.2(17.98) ± .10	0.69	3.83	36	16.5–20.3(18.21) ± .13	0.83	4.55
4. San Benito Is.	11	16.8–21.4(18.58) ± .42	1.41	7.58	12	16.0–20.5(18.25) ± .40	1.40	7.67
5. Guadalupe Is.	27	17.4–21.2(19.32) ± .19	1.00	5.17	22	18.4–21.3(19.85) ± .16	0.77	3.87
Bill Depth								
1. Northern Channel Islands	10	5.8–6.4(6.17) ± .09	0.28	4.53	8	5.4–6.5(5.92) ± .11	0.31	5.23
2. Southern Channel Islands	1	5.9			2	5.9, 5.9		
3. Los Coronados	41	5.6–6.5(6.09) ± .03	0.24	3.94	37	5.5–6.4(5.97) ± .03	0.23	3.85
4. San Benito Is.	12	5.3–6.1(5.75) ± .08	0.29	5.04	12	5.3–6.3(5.73) ± .08	0.28	4.88
5. Guadalupe Is.	28	5.2–6.1(5.78) ± .05	0.27	4.67	22	5.2–6.3(5.64) ± .05	0.27	4.78
Bill Ratio								
1. Northern Channel Islands	10	.31–.42(.35) ± .01	0.04	11.4	7	.26–.37(.33) ± .01	0.03	9.09
2. Southern Channel Islands	1	.36			2	.32–.37(.34)		
3. Los Coronados**	37	.31–.38(.34) ± .003	0.01	2.94	36	.30–.36(.32) ± .002	0.01	3.12
4. San Benito Is.	11	.26–.36(.31) ± .02	0.02	6.45	12	.28–.41(.31) ± .01	0.03	10.71
5. Guadalupe Is.**	26	.26–.34(.29) ± .003	0.01	3.44	21	.25–.32(.28) ± .003	0.01	3.57
Wing								
1. Northern Channel Islands	10	115–124(120.3) ± .94	3.00	2.49	8	119–126(122.5) ± .68	1.93	1.57
2. Southern Channel Islands	1	110			2	115–117(116)		
3. Los Coronados	44	115–125(119.1) ± .41	2.66	2.23	37	115–127(120.0) ± .53	3.20	2.66
4. San Benito Is.	13	111–123(118.5) ± .87	3.15	2.65	12	115–125(120.5) ± .84	2.91	2.41
5. Guadalupe Is.	29	114–128(119.3) ± .72	3.87	3.24	23	115–127(120.5) ± .66	3.18	2.63
Tarsus								
1. Northern Channel Islands	10	23.4–25.5(24.5) ± .21	0.67	2.73	8	23.8–26.0(24.9) ± .28	0.75	3.01
2. Southern Channel Islands	1	23.8			2	23.5–25.8(24.6).		
3. Los Coronados	40	22.9–25.3(24.2) ± .08	0.52	2.14	37	22.3–25.5(24.4) ± .11	0.67	2.74
4. San Benito Is.	13	22.4–25.2(23.6) ± .26	0.93	3.94	12	22.0–26.9(23.9) ± .34	1.17	4.89
5. Guadalupe Is.	29	21.2–25.4(23.5) ± .15	0.85	3.61	23	21.8–27.5(23.8) ± .27	1.32	5.54
Weight								
1. Northern Channel Islands	8	150–185(166.1)			5	156–184(173.2)		
4. San Benito Is.	9	134–161.5(148.0)			8	130–162.5(148.4)		
5. Guadalupe Is.	8	138–177(153.4)			8	148–185(168.1)		

**Sexual size differences significant at $P < 0.01$

Guadalupe population. The situation on the San Benitos is discussed below.

Northern populations.—Plumage characters do not allow separation of Channel Islands and Los Coronados birds. However, males from Los Coronados have significantly longer and thinner bills; significant size differences are not demonstrable among females, although the general trends noted above persist (Table 2).

TABLE 2. A statistical comparison (t-test) of size characters among several populations of Xantus' Murrelet *(Endomychura hypoleuca)*. Values for males are given to the top and right, for females to the bottom and left.

		Channel Is.	Los Coronados	San Benitos	Guadalupe
	Bill Length		P<.001	P<.001	P<.001
	Bill Depth		NS	.01>P>.001	P<.001
Channel Is.	Ratio		.01>P>.001	P<.001	P<.001
	Wing		NS	NS	NS
	Tarsus		NS	.05>P>.02	.02>P>.01
	Bill Length	NS		.1>P>.05	P<.001
	Bill Depth	NS		.01>P>.001	P<.001
Los Coronados	Ratio	NS		P<.001	P<.001
	Wing	NS		NS	NS
	Tarsus	NS		.02>P>.01	P<.001
	Bill Length	NS	NS		.1>P>.05
	Bill Depth	.02>P>.01	.01>P>.001		NS
San Benitos	Ratio	NS	NS		.02>P>.01
	Wing	NS	NS		NS
	Tarsus	NS	NS		NS
	Bill Length	P<.001	P<.001	P<.001	
	Bill Depth	.02>P>.01	P<.001	NS	
Guadalupe	Ratio	P<.001	P<.001	.01>P>.001	
	NS	NS	NS		
	NS	NS	NS		

Guadalupe Island.—As Green and Arnold (1939) reported, face pattern distinguishes the Guadalupe Island population *(hypoleuca)* from populations on more northern islands *(scrippsi)*. In Guadalupe birds the white of the face extends up in front of (and occasionally over) the eye, and onto the ear coverts; this condition is also present in the downy young. All but one of the specimens we examined had a face pattern of Class "0" or "1", the exception being a female that "had laid" taken by the POBSP in April 1968. Jehl has examined over 80 living murrelets at Guadalupe, either taken from nesting burrows or captured aboard ship, and all were "white-faced." Guadalupe birds also have longer, thinner bills than other populations of Xantus' Murrelet, and in bill size and proportions more closely resemble *craveri*.

Mensural differences alone are sufficient to distinguish the Guadalupe population. Males differ significantly from Channel Islands and Los Coronados birds in bill length, bill depth, bill ratio, and tarsus length, and females differ in bill length, bill depth, and bill ratio. As would be expected, the Guadalupe population shows fewer differences from the mixed San Benitos population; nevertheless, bill depth of Guadalupe males is significantly less, and females are significantly longer and thinner billed (Tables 1, 2).

The San Benitos.—The situation on the San Benitos is complicated in that birds typical of both *scrippsi* and *hypoleuca*, as well as intermediates, are present and apparently breeding. Van Rossem (1939) failed to appreciate the mixed nature of this population and described it as a new race, *pontilus*, which he said differed from *scrippsi* "in having the inner webs of the outer primaries with a light brown area next to the shaft; neck outline between dorsal and ventral areas very close to that of *Brachyramphus hypoleucus craveri* (Salvadori); bill shape intermediate between *scrippsae* (sic) and *craveri*, but perhaps closer to the former."

San Benitos birds are, on the average, thinner billed than those from more northern populations (Table 1), but are stouter billed than Guadalupe birds. However, we are unable to confirm the other differences alleged by van Rossem. Our

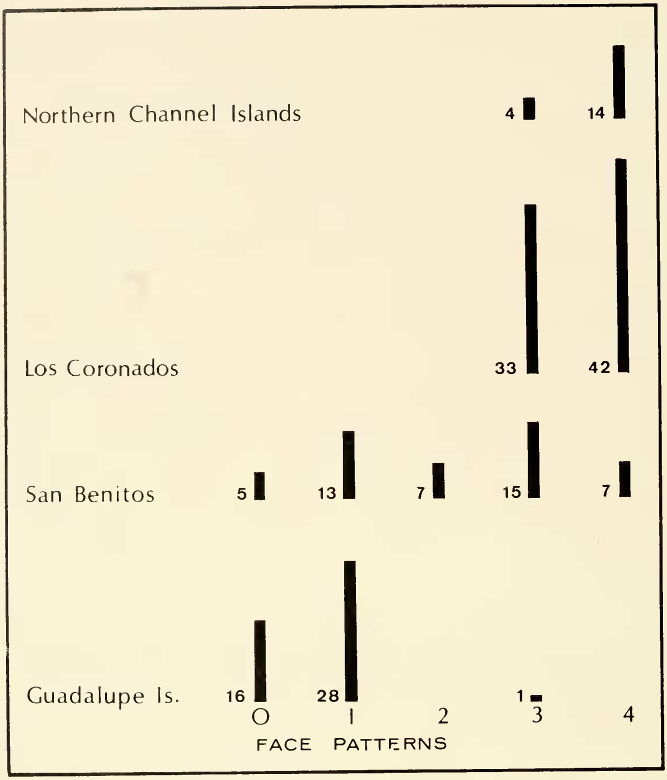

Figure 3. Geographic variation in face patterns among breeding populations of *Endomychura hypoleuca.* Character states (0-4) are illustrated in Figure 2.

sample included 7 of the 10 specimens on which he based his new race (type not examined), and from these it is clear that the alleged ventral extension of the dark collar is due to the make of the skins — in this case with the neck highly compressed. We can determine no differences in primary pattern among birds of any of the several populations.

San Benitos birds average intermediate in size between the Los Coronados and Guadalupe Island Populations, yet in several characters differ significantly from those populations (Table 2). Note, also, that variation in most characters is higher than elsewhere — which is further evidence of the composite origin of this population. Perhaps the greatest variability is shown in face pattern, which encompasses the entire range of variation in the species (Figs. 3, 4).

Sexual dimorphism.—Females of *E. hypoleuca* tend to have longer bills, wings, and tarsi than males but the differences are not significant. Bill depth of males averages greater, and in the Guadalupe and Los Coronados populations males are significantly heavier-billed ($P<.01$) than females. There are no sexual differences in coloration (Table 1).

Endomychura craveri

Measurements of Craveri's Murrelets are given in Table 3. The sample was subdivided into specimens from three probable breeding areas: Northern Gulf of

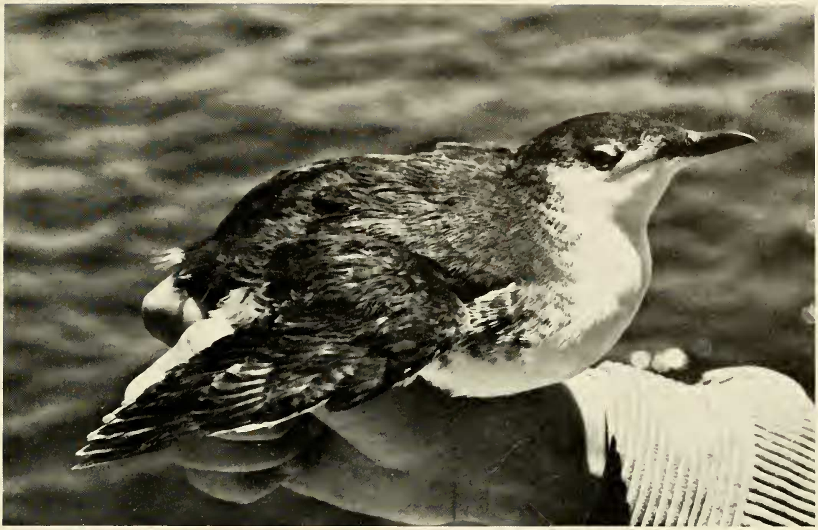

Figure 4. An example of *Endomychura hypoleuca* with an intermediate face pattern ("2"), captured aboard ship at the San Benito Islands, 26 May 1971.

California (islands off Baja California Norte), Southern Gulf of California (islands off Baja California Sur), west coast of Baja California (Magdalena Bay to Cabo Colnett). A fourth sample comprises birds collected off northern Baja California and California following the breeding season.

No statistical differences or trends in mensural characters could be demonstrated among the three putative breeding populations, and the data from all areas were combined. No plumage differences are evident. The face pattern is uniform (Class "5") in all populations. There is considerable variation in underwing coloration, but because of the make of the skins this character could not be analyzed in detail — it does not seem to vary geographically.

Post-breeding birds from northern Baja California and California differ significantly from breeding populations: 1) males and females average longer-billed ($P<.001$); 2) the bill depth of males averages smaller ($.01>P>.001$); 3) the bill ratio is smaller in both sexes ($P<.001$); 4) and post-breeding birds tend to have longer wings (males, $.1>P>.05$; females, $.05>P>.02$). The vast majority of these birds were collected in Monterey Bay in the autumns of 1907 and 1909. Since it is untenable to suggest that they were derived from a morphologically distinct but unknown breeding population, the differences could reflect a) selection for larger birds to disperse more widely (Monterey is near the northern limit of the species' range), or b) differences in the age composition of the post-breeding sample. The second alternative seems likely, as the Monterey population doubtless includes immatures as well as adults. We attribute the relatively shallow bill of the Monterey sample to the presence of juveniles, whole bill growth was incomplete. Longer wings probably result from a recent molt. The relatively long bill is less easy to explain. Breeding birds suffer extensive wear of the body plumage and, probably, bill tip as well, as they scramble among rocks and into their nest crevices. We suspect that the "increased" bill length is merely a return to unworn dimensions. Bill lengths of birds taken in September off Monterey average 0.4 mm longer than those taken in August.

Sexual dimorphism.—As in *E. hypoleuca*, bill length and tarsus length average

TABLE 3. Measurements of Craveri's Murrelet *(Endomychura craveri)*

Area	Male No.	Male Range, mean and S.E.	Male S.D.	Male C.V.	Female No.	Female Range, mean and S.E.	Female S.D.	Female C.V.
		Exposed Culmen						
1. Northern Gulf of California	11	18.6–21.3(19.95) ± 0.23	0.78	3.90	11	18.2–21.9(19.80) ± 0.30	1.02	5.15
2. Southern Gulf of California	21	18.0–22.5(19.77) ± 0.22	1.04	5.26	10	18.6–21.8(19.99) ± 0.33	1.04	5.20
3. West Coast of Baja California	10	19.0–21.0(19.67) ± 0.24	0.73	3.70	8	18.7–21.2(19.72)		
Areas 1-3	42	18.0–22.5(19.80) ± 0.14	0.92	4.64	29	18.2–21.9(19.86) ± 0.19	1.00	5.03
4. California and Northern Baja California	34	18.0–21.7(20.87) ± 0.10	0.78	3.73	21	19.1–22.4(20.99) ± 0.17	0.81	3.85
		Bill Depth						
1. Northern Gulf of California	11	5.3–5.9(5.56) ± 0.05	0.19	3.41	10	5.2–5.7(5.43) ± 0.04	0.14	2.57
2. Southern Gulf of California	22	4.9–5.8(5.39) ± 0.05	0.23	4.26	10	5.0–5.6(5.27) ± 0.18	0.18	3.41
3. West Coast of Baja California	9	5.1–5.6(5.37) ± 0.04	0.14	2.61	8	4.9–5.7(5.31)		
Areas 1-3*	43	4.9–5.9(5.43) ± 0.03	0.22	4.05	28	4.9–5.7(5.34) ± 0.03	0.18	3.38
4. California and Northern Baja California	35	4.7–5.7(5.28) ± 0.03	0.23	4.35	24	4.6–5.7(5.25) ± 0.05	0.26	4.95
		Bill Ratio						
1. Northern Gulf of California	11	0.25–0.31(0.27) ± 0.005	0.01	3.70	11	0.25–0.30(0.27) ± 0.004	0.01	3.70
2. Southern Gulf of California	21	0.24–0.30(0.27) ± 0.003	0.01	3.70	10	0.25–0.29(0.26) ± 0.004	0.01	3.84
3. West Coast of Baja California	10	0.24–0.29(0.27) ± 0.004	0.01	3.70	8	0.25–0.30(0.27)		
Areas 1-3	42	0.24–0.31(0.27) ± 0.002	0.01	3.70	29	0.25–0.30(0.27) ± 0.002	0.01	3.84
4. California and Northern Baja California	34	0.21–0.29(0.25) ± 0.002	0.01	4.00	22	0.23–0.27(0.25) ± 0.002	0.01	4.00
		Wing						
1. Northern Gulf of California	11	112–123(116.6) ± 0.98	3.28	2.81	12	115–122(118.7) ± 0.60	2.02	1.70
2. Southern Gulf of California	21	107–119(115.4) ± 0.74	1.43	1.24	10	111–123(117.8) ± 1.11	3.51	2.97
3. West Coast of Baja California	9	111–121(116.5) ± 1.11	3.15	2.71	8	116–119(117.5)		
Areas 1-3*	41	107–123(116.1) ± 0.49	3.08	2.65	30	111–123(117.8) ± 0.49	2.59	2.18
4. California and Northern Baja California	36	111–122(117.4) ± 0.43	2.63	2.24	26	114–124(118.9) ± 0.56	2.85	2.39
		Tarsus						
1. Northern Gulf of California	11	21.9–23.5(22.67) ± 0.15	0.51	2.25	11	22.4–23.8(22.88) ± 0.13	0.43	1.88
2. Southern Gulf of California	22	21.0–24.4(22.95) ± 0.17	0.82	2.78	10	22.0–24.1(22.96) ± 0.22	0.71	3.09
3. West Coast of Baja California	10	21.8–24.4(23.29) ± 0.27	0.82	3.53	8	22.6–24.4(23.27)		
Areas 1-3	43	21.0–24.4(22.93) ± 0.12	0.78	3.40	29	22.0–24.4(23.01) ± 0.11	0.60	2.60
4. California and Northern Baja California	34	21.4–24.4(23.04) ± 0.11	0.66	2.86	26	22.2–24.5(23.24) ± 0.11	0.57	2.45
		Weight						
Area 3 (San Benito Is. April-May)	6	128–149(137.1)			5	131–137(134.8)		

*Sexual size differences significant at $P < 0.05$

greater in females, and wing length is significantly greater ($.05 > P > .01$). Among breeding populations bill depth of males is greater ($.05 > P > .02$), and there is a tendency for the bill ratio to be larger as well. There are no sexual differences in coloration (Table 3).

DISCUSSION

As shown above, size varies clinally in *E. hypoleuca*, birds in the southern part of the range having longer and thinner bills but shorter wings and tarsi. These trends are, in all cases, toward the condition shown by *E. craveri* (cf. Tables 1, 3). On the other hand, *craveri* shows no geographic variation in size, and specifically *does not* show trends toward *hypoleuca (sensu lato)* as it approaches the zone of contact. This fact, plus the absence of intergradation in face pattern or underwing coloration in the mid-peninsula region, indicates that *hypoleuca* and *craveri* are behaving as distinct species — a conclusion that gains support from field observations of assortatively mated pairs in this area.

If hybridization between *hypoleuca* and *craveri* is occurring, it seems to be extremely rare. Van Rossem (1939) considered an unsexed specimen from Natividad Island, collected on 9 April 1897, (now Carnegie Mus. 22965) "exactly intermediate in all particulars . . ." Unaware of van Rossem's opinion, we independently discovered this specimen and noted its unusual combination of characters. Its measurements (exposed culmen 19.4 mm; bill depth 5.1 mm; bill ratio 0.26; wing 111 mm; tarsus 22.2 mm), with one exception, are within the range of either species, though much closer to the mean values for *craveri;* bill depth is smaller than that of any *hypoleuca* examined. Its face pattern and brownish tinge to the back are also like that of *craveri* and the undersides of the outer primaries are dark. However, the ventral extension of the collar seems less pronounced than in most examples of *craveri* and the underwing is mainly white, with only a few grayish feathers, as in *hypoleuca.* The specimen is certainly closer to *craveri,* but we suspect that it is of hybrid origin.

The taxonomic status of Xantus' Murrelet populations is less clear. *E. h. hypoleuca* and *E. h. scrippsi* are as distinct from each other morphologically as either is from *E. craveri* and on that basis two species of "Xantus'" murrelets might be recognized. However, these forms evidently interbreed where they come in contact, because intermediate face patterns (Class "2") occur only in the San Benitos. Although the categorization of face patterns is subjective, it is evident that the distribution of face pattern character states is strongly bimodal, with parental types (Classes "0" and "1" vs. "3" and "4") predominating (Figure 3). (In this population bill length, bill depth, and bill ratio are strongly correlated with face pattern [$P \cong .01$; $.05 > P > .01$; and $P > .01$ respectively] but bimodality cannot be demonstrated in those characters because of extensive overlap in dimensions between the parental populations). This indicates non-random mating and suggests that some isolating mechanisms between these populations are operating. Whether interbreeding will lead to strengthening of the isolating mechanisms or to swamping of populational differences is uncertain. For the time being, we consider it preferable to continue to recognize *hypoleuca* and *scrippsi* as well-marked races of Xantus' Murrelet, realizing that the divergence may have already passed that stage.

One difficulty in analyzing the San Benitos situation is the lack of historical information. Birds with intermediate face patterns were present in the 1890's, but the earliest collection of *E. h. hypoleuca* there was in 1968, and this form now comprises a large fraction of that population (Fig. 3). Green and Arnold (1939) and DeLong and Crossin (MS) both mention that breeding colonies on islets at Guadalupe Island appear overcrowded, and it may be that birds have shifted to the San Benitos — the nearest alternate breeding site — very recently.

Isolating Mechanisms

If *E. craveri* and *E. hypoleuca* are distinct species what isolating mechanisms are fuctioning to restrict interbreeding? We know very little about the breeding behavior of these birds, but the following might be involved.

Voice.—Murrelets are vocal at sea during the breeding season, especially at night when singing birds congregate on the water near breeding colonies. The "song" is a trilling whistle given on one pitch which to Jehl's ear is slightly drier and less musical in *craveri*. These songs are so similar that we doubt they play any role in species recognition, but further analysis is warranted.

Timing of the breeding season.—Straggering of the breeding seasons is a potentially useful mechanism for reducing the potential for interbreeding among closely related, sympatric species. In the Gulf of California Craveri's Murrelets apparently begin to pair in late December; chicks have been reported as early as March and large young as late as June. The peak of hatching in most years probably occurs in April (DeWeese and Anderson, MS). Xantus' Murrelets in California nest much later. Egg dates (376 sets) on Los Coronados range from 4 April to 6 July, with the peak of laying from 15 to 20 May. Similar periods have been recorded for the Channel Islands. At Guadalupe, nesting is slightly earlier, the peak of laying occurring between mid-April and early May.

Breeding phenology on the San Benitos is less clear. We know of seven sets of eggs taken between 10 March and 26 April; Kaeding (1905) also reported nests in late March. Presumably these records all pertain to *hypoleuca*, as all of the specimens that we have examined from these islands taken prior to 1968 were collected in March and all were Xantus'. Further, Kaeding specifically stated that none of the birds he saw had characters of *craveri*. In the winters of 1971-1973, staff members of the San Diego Natural History Museum made weekly visits to the San Benitos from mid-January to mid-March. Casual observations indicated that singing murrelets had congregated near the islands by January, but all that were captured aboard ship or identified in the ship's lights were reported as Xantus'. Our earliest record of *craveri* is a bird found dead in a life boat on 4 April 1971. By late April and May however, *craveri* seems to comprise 20–30% of the population. These data are insufficient to prove asynchronous nesting. But if *craveri* does nest on the San Benitos, its nesting period seems retarded as compared to the Gulf population, and later than that of *hypoleuca* in the area of overlap.

Face pattern and bill shape.—Although *Endomychura* murrelets lack the facial plumes and bill ornamentation that are highly developed in many other alcids, differences in face pattern and bill shape are sufficient to allow rapid species identification and to function as isolating mechanisms. *E. craveri* and *E. h. scrippsi* have similar face patterns but distinct bill shapes. Bill shapes of *craveri* and *E. h. hypoleuca* are similar, but these taxa differ completely in face pattern. A combination of face and bill characters distinguishes *E. h. hypoleuca* from *E. h. scrippsi.* The ranges of these three taxa are essentially parapatric, and it is conceivable that the differences among the several populations constitute a complex pattern of character displacement.

Relationships of *Endomychura*

Many authors have treated *Endomychura* as a synonym of *Brachyramphus*, and that merging has recently been re-advanced, without justification, by Mayr and Short (1970). Yet, as long ago as 1945, Storer showed that morphology, plumage, and nesting habits clearly separated the Marbled and Kittlitz' murrelets *(B. marmoratus* and *B. brevirostris)* from other murrelets including *Endomychura*, and that *Endomychura* was more closely allied to *Synthiloboramphus* than to other alcid genera. Storer's position is further confirmed by the color patterns of the downy young, which form an almost perfectly graded series from *Synthilobor-*

Figure 5. The downy young of *Synthiloboramphus antiquus*, *Endomychura hypoleuca hypoleuca*, *E. h. scrippsi*, and *E. craveri*.

amphus to *craveri* (Fig. 5), and which differ markedly from the color patterns of *Brachyramphus* chicks (Thompson, Hines, and Williamson, 1966; Singer and Verardo, 1975). In *Synthiloboramphus* chicks the dorsum is extensively reduced with gray, resulting in a frosty appearance; the frosting is progressively reduced in *E. h. hypoleuca* and *E. h. scrippsi* and is lost in *E. craveri*. A similar cline is evident in face pattern: *Synthiloboramphus* shows a white postocular spot that is separated from the whitish venter by a thin dark line; in *E. h. hypoleuca* the line is absent but the white of the underparts extends up behind the eye; in *E. h. scrippsi* and *E. craveri* the post-orbital spot has been lost.[2]

Perhaps of greater interest is that the adult morphology of *Synthiloboramphus* also fits the general pattern of geographic variation in *Endomychura*. Considering *Synthiloboramphus-Endomychura* as an evolutionary unit, we find a rough cline from a relatively large (long-winged, long-legged) but short and deep-billed murrelet in the north *(Synthiloboramphus)* to a smaller (shorter wings and tarsi) but longer and thinner-billed southern form *(craveri;* Table 4).

Recently, Cody (1973) has attempted to analyze the structure of alcid communities in ecological terms (see Bedard, in press, for a critique of Cody's approach). It should be obvious that success in modeling community structure depends upon knowledge of the *biology* of the component species and a firm understanding of their evolutionary histories. In the present case, the reasons for the pattern of clinal variation shown in *Synthiloboramphus-Endomychura* remain to be determined. While they might involve the effects of selection from potential competitors, it seems more likely that they reflect the operation of the well-known (if controversial) "Ecogeographic Rules" of Bergmann and Allen.

[2]In a paper received while this paper was in galleys, Binford, Elliott, and Singer (1975, Wilson Bulletin, 87: 303-319) described the young of *Brachyramphus marmoratus* and compared it with chicks of *Synthiloboramphus* and *Endomychura*. The taxonomic conclusions they reached are identical to ours.

TABLE 4. Patterns of Morphological Variation in *Synthiloboramphus-Endomychura*

Taxon	Culmen	Bill Depth	Bill Ratio	Wing	Tarsus
	Mean dimensions (mm)[1]				
S. antiquus	13.2	6.55	.49	135	26.5
E. h. scrippsi	17.0	6.17	.35	120.3	24.5
E. h. hypoleuca	19.3	5.78	.31	118.5	23.5
E. craveri	19.8	5.43	.27	116.1	22.9

[1]Dimensions for *Synthiloboramphus* based on Ridgway (1919) and specimens in San Diego Natural History Museum; for *Endomychura* data are abstracted from Tables 1 and 2 (males only).

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APPENDIX I

Specimens examined

Endomychura craveri

Northern Gulf of California: Tiburon Island and vicinity-12; Partida Island-3; Bahía de los Angeles-3; San Esteban Island-1; Pond Island-3. Dates: 8 March – 20 April.

Southern Gulf of California: Ildefonso Island and vicinity-17; San Francisco Island-5; San José Island-16; Roca El Cayo-1; Puerto San Carlos, Sonora-1. Dates: 6 February – 1 May.

West Coast of Baja California: Bahía San Juanico-1; Magdalena Bay-1; San Benito Islands-12; Pequina Point (near San Ignacio Lagoon)-1; Cedros Island-1; Cabo Colnett-1; San Martín Island-1. Dates: 8 February – 13 June.

California and Northern Baja California (post-breeding): Oregon-1; Monterey Bay, Ca.-29; Catalina Channel, Ca.-1; Off San Diego and Los Coronados-2; Off San Pedro, Ca.-1; Los Angeles County, Ca.-1; Off Pta. San Ysidro, B. C.,-1; San Martín Island, B. C-1. Dates: 4 August – 6 October.

Endomychura hypoleuca

California: Prince Islet, San Miguel Island-13; Anacapa Island-5. 6 May – 4 June.

Baja California: Los Coronados-87; San Benito Islands-25 (plus 22 banded); Guadalupe Island-54. 11 February – 13 July.

Non-breeding birds. Off Washington State-1. California: Monterey Bay-24; Santa Cruz Island-1; Santa Barbara Island-2; Off San Luis Obispo-1; Santa Catalina Island-2; Catalina Channel-2; Los Angeles County-7; Orange County-1; Off San Diego-8. Baja California: Off Northern Baja California-1; 150 mi NW Guadalupe Island-1. Dates: Entire year, but mainly late summer-early spring.

APPENDIX II

Distribution of *Endomychura* murrelets

Endomychura craveri.—Breeds on islands in the Gulf of California from Consag Rock to Isla del Espiritu Santo (DeWeese and Anderson, MS). Probably breeds on islands along the west coast of Baja California from Magdalena Bay (Sta. Margarita Island) to the San Benitos (this paper), and perhaps slightly farther northward. Post-breeding birds wander northward, irregularly, to Monterey, California; one Oregon record (Jehl, in press). April sight record off Guatemala (Jehl, 1974).

Endomychura hypoleuca hypoleuca.—Breeds on Guadalupe Island, Baja California, and presumably on the San Benitos, where it hybridizes with *E. h. scrippsi.* Post-breeding distribution poorly known. Type specimen taken off Cabo San Lucas, B. C. in mid-July. Apparently wanders regularly to southern California (specimen 150 mi NW Guadalupe Island; 2 juveniles from Catalina Channel, Ca.) and perhaps well beyond. Two birds (mated pair?) taken well off Cape Flaherty, Wash. (Cowan and Martin, 1954) are referable to this race (racial identity determined by us).

Endomychura hypoleuca scrippsi.—Breeds or formerly bred on near-shore island, of California and Baja California, from Prince Islet, San Miguel Island, to the San Benitos. Apparently extirpated on the Todos Santos Islands and San Martín and perhaps elsewhere. May have formerly bred on Natividad Island. After breeding, ranges to northern California, occasionally to Oregon and Washington (Scott et al., 1971; Sanger, 1973 [specimen examined by us]; Feinstein, 1958 [specimen examined by us]).

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